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The palaeoenvironment of the middle Miocene pliopithecid locality in Damiao, Inner Mongolia, China

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Abstract

Damiao, Inner Mongolia has three main fossil horizons representing early, middle and late Miocene. The middle Miocene locality DM01 is the only primate locality from the region and also represents the latest occurrence of pliopithecoids in north China. The presence of pliopithecoid primates in central Asia after the middle Miocene climatic optimum seems to contradict the general trend of strengthening climatic zonality and increasing aridity. To investigate this enigma we employ faunal similarity, ecometrics, and stable isotope analysis. Our results support previous inferences concerning the presence of locally humid environments within the increasingly arid surroundings that characterized Central Asia. Hypsodonty, estimated mean annual precipitation (MAP), local sedimentology and large mammal fossils suggest more humid and possibly more forested and wooded environments for the DM01 locality. We compared our results with the adjacent fossil-rich middle Miocene Tunggur localities. However, the small mammal fauna and isotope data are consistent with a mosaic of forest and grassland environment for all Damiao localities. Based on our results Tunggur may have been too seasonal or not sufficiently humid for pliopithecids. This is supported by the higher mean hypsodonty and lower predicted MAP estimates, as well as slightly higher δ^{13}C values. We suggest that DM01, the driest known Asian pliopithecid locality, may have been a more humid refugium within a generally drier regional context.

Keywords: stable isotopes, ecometrics, hypsodonty, precipitation, faunal similarity, Nei Monggol,

Introduction

Central Inner Mongolia is well known for its fossil-rich Neogene terrestrial deposits that have attracted the attention of palaeontologists since the early years of the 20th Century (e.g., Andersson, 1923; Teilhard de Chardin, 1926a, b; Andrews, 1932). However, until the discovery of a pliopithecid primate from the middle

Miocene locality of Damiao in 2006, no Miocene primates were known from the region. This is also the latest occurrence of pliopithecoids in Central Asia, excluding the putative *Pliopithecus posthumus* (Schlosser, 1924), from Ertemte, Inner Mongolia (ca. 5-6 mega-annum (Ma), the primate status of which has been questioned (e.g., Hürzeler, 1954; Simons, 1972; Simons and Fleagle, 1973; Harrison et al., 1991; Harrison and Gu, 1999; Harrison, 2005) and is not discussed here further. Neither do we discuss other northern Chinese primate localities, such as Tongxin (Ningxia Hui Autonomous Region), Tabenbuluk nor Yindirte (Gansu Province) that are older than Damiao (late Oligocene to middle Miocene) (Bohlin, 1946; Harrison et al., 1991). The particular palaeoecological conditions of pliopithecoids are not yet known but Eronen and Rook (2004), and Sukselainen et al. (2015) suggest that they preferred humid subhabitats. The presence of pliopithecid primates in central Asia after the middle Miocene climatic optimum is particularly interesting since it seems to contradict the general trend of strengthening climatic zonality and increasing aridity from the early Miocene onwards (Kaakinen et al., 2015).

We approach this question using faunal similarity, ecometric analysis, and stable isotope analysis. Faunal similarity is generally used as a measure of faunal provinciality (e.g., Bernor, 1978, 1983; Fortelius et al., 1996; Nargolwalla, 2009). Here we use genus-based faunal resemblance to detect similarities between localities in a geographically and temporally restricted area. Our rationale is that significant differences between contemporaneous faunas may indicate the presence of restrictive barrier between localities, such as water, climate or vegetation (Middlemiss and Rawson, 1969; Raup and Crick, 1979; Simpson, 1940). As an ecometric proxy for humidity we use the mean ordinated molar crown height (hypsodonty) of large herbivorous mammals, which has previously been shown to correlate with precipitation and humidity (e.g., Fortelius et al., 2002, Eronen et al., 2010a). We also estimate the mean annual precipitation (MAP) based on the herbivorous large mammal community structure and their dental traits. We use carbon isotope ratios of enamel in herbivorous mammals to show the extent to which their diet was composed of C3 or C4 vegetation. We further use oxygen isotope compositions of fossil tooth enamel to reconstruct palaeoclimate, (Kohn et al., 1996) especially past aridity (Longinelli, 1984; Fricke et al., 1998; Levin et al., 2006). In this study we investigate the occurrence of pliopithecids, a group that typically favours humid

environments in the context of regional drying trends (for general overview see e.g. Fortelius et al. 2014). Why do pliopithecids occur at Damiao when they are absent from the similar fossil-rich and intensively collected neighbouring locality of Tunggur?

Environmental context in Eurasia

The Neogene (23-2.6 Ma) of Eurasia can be characterized by three climatically distinct periods: (1) the warm and humid early Miocene (23-17 Ma) with weak seasonality and low temperature gradients (Utescher et al., 2000; Mosbrugger et al., 2005; Bruch et al., 2007, 2011); (2) the middle Miocene climatic optimum (17-15 Ma); and (3) the subsequent cooling that led a trend towards more arid and open habitats in the late Miocene and Pliocene (Zachos et al., 2001, 2008; Fortelius et al., 2014; Song et al., 2014).

The climate in eastern Asia was dominated by the planetary system throughout most of the Miocene until the latest Miocene when the uplift of the Tibetan Plateau strengthened the regional monsoon system (An et al., 2001; Passey et al., 2009; Liu et al., 2009; Tang et al., 2011, 2013). The climate in China at 17-13.5 Ma was relatively humid showing no clear pattern of a latitudinal gradient in humidity (Liu et al., 2009). Between 13.5 Ma and 11.1 Ma, the latitudinal climate gradient increased and arid belts appeared in the mid-latitudes of Asia, while in the north and south humid conditions continued to prevail (Flower and Kennett, 1994; Liu et al., 2009; Mirzaie Ataabadi et al., 2013). There is no consensus on whether North China was humid during this time (see e.g. Sun et al., 1998; Guo et al., 2002; Sun and Wang, 2005; Liu et al., 2009), but it has been suggested that humid conditions may have occurred locally within a more arid regional environment, such as in riverine corridors (Kaakinen et al., 2015; Wang and Zhang, 2011).

Pliopithecids

Pliopithecidae was a diverse family that during the Miocene ranged widely throughout Eurasia from the Iberian Peninsula to eastern China. They were also among the first fossil primates to be discovered and described (e.g., Lartet, 1837; Biedermann, 1863; Hofmann, 1893; Ginsburg and Mein, 1980; Ginsburg, 1986; Andrews et al., 1996; Harrison and Gu, 1999; Begun, 2002; Alba et al., 2010; Harrison, 2013). The earliest known occurrence of pliopithecids is from the late early Miocene (ca. 17-18 Ma) of Sihong, Jiangsu, China. These are the two oldest and most primitive genera of pliopithecids, *Dionysopithecus* and *Platodontopithecus* (Li, 1978; Harrison and Gu, 1999; Begun, 2002). More specialized pliopithecines were likely to have originated from these early Asian forms, later dispersing into Europe. Previously, the more derived and late-surviving pliopithecids, the crouzeliines, were thought to have originated from these European forms (Harrison and Gu, 1991; Moyà-Solà et al., 2001; Alba et al., 2010) but new evidence of primitive crouzeliines from Fanchang, east China implies that may have originated in Asia prior to arriving in Europe (Harrison, 2013). During the middle Miocene, ca. 15-12 Ma, pliopithecids are known from several Chinese localities; Laogou, Gansu Province; Junggar Basin, Xinjiang Autonomous Region; Tongxin, Ningxia Hui Autonomous Region; and Damiao, Inner Mongolia (Harrison et al., 1991; Wu et al., 2003; Deng, 2003; Begun, 2002; Zhang and Harrison, 2008). The latest known occurrence of pliopithecids is also from China, from the late Miocene locality of Shihuiba, Lufeng, Yunnan where they co-existed with hominoids at ca. 6.9-6.2 Ma (Dong and Qi, 2013).

The distribution of pliopithecoids as a clade reflects an ecological preference for more persistently humid habitats than those inferred for other contemporary primate clades (Eronen and Rook, 2004; Sukselainen et al., 2015), but not much is known about the ecological preferences of each species. Unlike hominoids, they did not adjust their habitat preferences to the increasingly arid conditions of the Miocene, but effectively remained in their ancestral ecological and climatic niche (Sukselainen et al., 2015). In the late middle Miocene of Asia pliopithecids are absent from mid-latitudes and are recorded only from north China, at Damiao, Inner Mongolia (Zhang and Harrison, 2008; Kaakinen et al., 2015).

Study area

Damiao is located in Siziwang Banner, central Inner Mongolia, ca. 100 km north of the provincial capital of Hohhot. Following its discovery in 2006, the site was excavated during three field seasons (until 2009). There are three main fossil-bearing horizons with more than 30 mammal localities, the majority of which occur within a few square kilometres ca 65 km north of Ulanhua town (Figure 1). Three of the most productive localities (DM16, DM01 and DM02) are magnetostratigraphically dated to range from early Miocene to earliest late Miocene (Kaakinen et al., 2015). In addition, late Miocene ages can be tentatively inferred for fossils for DM06, DM12, DM13, and DM26, and late late Miocene for the southernmost locality, the so-called "UH Museum". The northernmost locality, DM17, is provisionally considered as representing late Eocene in age.

FIGURE 1

The stratigraphically lowest locality, DM16, is dated to 20-21 Ma, and has mainly yielded small mammal remains. The DM16 strata are characterized by red-brown mudstone with thin horizontal laminations and desiccation cracks (Kaakinen et al., 2015). Fossil mammals from the richest locality, DM01, are biochronologically correlated with the late middle Miocene Tunggur fauna and are estimated to be 12.1 Ma (Kaakinen et al., 2015). This locality has more than 30 mammal species, including a pliopithecid primate (Zhang and Harrison, 2008). DM01 fossils come from a 1-1.5 m thick complex of carbonate nodule conglomerate and sandstone beds with distinctive manganese and iron staining. The exposed lateral extent of the locality is ca. 60 m (Zhang et al., 2012; Kaakinen et al., 2015). The DM02 locality is early late Miocene, with an estimated age of 11.6 Ma, and has produced mainly small mammal teeth that are found in a ca. 20 cm thick sandstone lying above mudstones (Kaakinen et. al., 2015). The depositional setting at Damiao is fluvial in nature with well-drained floodplains (Kaakinen et al., 2015); the large mammal community structure throughout the sequence shows a relatively stable pattern with cervoids predominating (Zhang et al., 2011; Kaakinen et al., 2015). Although the cervoids are not diagnostic of woodland environments, they probably exclude the possibility of exclusively grassland or desert environments for the Damiao sequence.

The Central Asiatic Expedition of the American Museum of Natural history discovered the site of Tunggur in 1928 (Spock, 1929; Andrews, 1932). Subsequent excavations resulted in huge collections of mammalian fossils, including *Platybelodon grangeri*, a shovel-tusked gomphotheriid (Wang et al., 2003; Wang et al., 2013). The Tunggur fauna, also known as the *Platybelodon* fauna, includes all assemblages from the Tunggur Formation and is the most diverse and abundant Chinese middle Miocene mammal assemblage. It is the basis for Tunggurian Land Mammal Stage/Age (LMS) in East Asia spanning from 11.8 Ma to 12.6 Ma (Qiu et al., 2013). The lateral extent of the fossil-bearing sediments in the Tunggur area (Figure 1) is several hundreds of square kilometres and includes several localities of similar age (e.g., Mandelin Chabu (MC), Aoershun Chaba (AC), Zhunwuguer (ZH), Wolf Camp (WC), Dabuhaer (DA), Platybelodon Quarry (PQ), Moergen, Aletexire (ALU), Huerguolajin (HU), Roadmark 482 (482), Tairum Nor, Tairum Nor middle sandstone (TMS)) (Wang et al., 2003). The palaeoenvironment of Tunggur has been investigated using several methods resulting in somewhat different interpretations. Pollen data from the northeastern part of the Tunggur tableland points to woodland habitats, mixed conifer and broadleaf trees, with small areas of shrub/grassland (Dong, 1993 in Wang et al., 2003). Arid grassland or possibly semidesert was suggested by Qiu (1996) based on the small mammal fauna. The large mammals on the other hand point to a mixed habitat of woodland and grassland (Colbert, 1939; Wang et al., 2003). Sedimentological analysis suggests small highly alkaline ponds and shallow meandering rivers (Wang et al., 2003). Isotopic analysis of fossil tooth enamel indicates water-stressed C3 diets that imply mixed habitats of woodland and C3 grasslands (Zhang et al., 2009). All these palaeoenvironmental proxies suggest a mosaic of different local environments for Tunggur with grassland and mixed conifer-broadleaf woodland, in an area with shallow meandering rivers and alkaline ponds during the dry season, much as in the present-day grasslands of the region (Zhang et al., 2011; Wang et al., 2003).

Material

Fossil mammal data for hypsodonty, precipitation, and similarity analysis were downloaded from New and Old Worlds (NOW) database on 20th October 2014 (Fortelius, 2014; http://www.helsinki.fi/science/now). We included Eurasian localities within the temporal range of MN04-MN12 (Mammal Neogene units following NOW database usage, see also Steininger 1999). Following Mirzaie Ataabadi (2010), *ad hoc* MN equivalents (MNEQ) are used instead of traditional MN units to make Eurasian mammal biostratigraphy provisionally uniform. MNEQ ages were assigned for each locality from the minimum and maximum locality ages as given in the NOW database. Only localities where both the maximum and the minimum ages fell within the boundaries of the MNEQ-unit were included (MNEQ sensu Mirzaie Ataabadi, 2010).

Tooth samples for isotopic analysis were collected during the 2007 and 2008 field seasons. For the analysis, enamel from 79 teeth of large herbivorous fossil and modern mammals were analysed. Of these specimens 52 were perissodactyls (i.e., rhinos and equids), 25 artiodactyls (i.e., bovids, cervids, one giraffid, and a few unidentified ruminants), and two proboscideans (gomphotheriids). The fossil material comes from twelve early to late Miocene localities. The late late Miocene Ulan Hua Red Clay Museum locality is situated near Wulanhua town, ca. 60 km south from the other Damiao localities. The modern sample consists of five bovids, including *Bos*, *Ovis*, and *Capra*.

Methods

Hypsodonty and precipitation

Hypsodonty is calculated as the ratio of height to length of the second upper or lower molar. It is a measure of dental durability and it has also been used increasingly as a proxy for humidity (Fortelius et al., 2002, 2003, 2006; Liu et al., 2009; Eronen et al., 2010a, 2010b, Mirzaie Ataabadi, 2010; Sukselainen et al., 2015). In the NOW database three classes of hypsodonty are recorded - brachydont, mesodont, and hypsodont. These are assigned numerical values 1, 2, and 3 (respectively) and from these ordinated scores, the mean hypsodonty values for large herbivorous mammals (Orders Artiodactyla, Perissodactyla, and Proboscidea)

were calculated for each locality following the method of Fortelius et al. (2002). Only localities that fell within one MNEQ unit and had more than one specimen available for hypsodonty scoring were included in the analysis.

Estimated mean annual precipitation was calculated using methods of Eronen et al. (2010a, 2010b), and Liu et al. (2012). The method of Eronen et al. (2010a) estimates precipitation using a regression tree analysis based on the mean (community-level) molar crown height of extant large herbivorous mammals and measured precipitation. The method of Liu et al. (2012) uses an ordinary least-squares linear regression model to estimate the mean annual precipitation from mean hypsodonty and longitudinal loph count. Both methods show similar trends in the estimated MAP. Since the Eronen et al. (2010a, b) method is more sensitive to sample size we focus on the method of Liu et al. (2012). We also note that we are mainly concerned about the relative change in aridity, and therefore do not focus on absolute precipitation estimates. For the current analysis we used the entire Eurasian data from the NOW database but we only discuss the relevant Chinese localities here. Results for both methods are shown in Table 1 for MNEQ06-09 Chinese localities and SOM1 for all analysed Eurasian localities.

Temporal changes of hypsodonty and MAP were inspected with respect to different types of localities. For the purposes of this study the following four locality types were identified: pliopithecoid localities, hominoid localities, other primate localities (with cercopithecoids, sivaladapids, tarsiids, lorisids, and/or indeterminate primates), and non-primate localities. The results are shown in graphs and tested using a pairwise Mann-Whitney test.

Faunal similarity metrics

Taxonomic presence/absence data from different localities can be used to estimate similarity between fossil localities. Different similarity indices have been employed (see Hammer and Harper, 2009 for a review). One of the simplest and oldest is Simpson's index = M/S, where M is the number of shared taxa

and S is the number of smaller taxa (Simpson, 1943). This method was chosen here since it is insensitive to the size of the sample and ignores absences in the smaller fauna. These qualities are desired for sample sizes that vary and because the Damiao samples are rather small. Analyses were run on PAST 3.01 (Hammer et al., 2001) separately for small and large land mammals. (The distinction between 'small' and 'large' land mammals is here purely taxonomic; small mammals include orders Eulipotyphla, Lagomorpha, and Rodentia, excluding the avian Chiroptera, all other terrestrial orders were considered large mammals.) Chinese localities between MNEQ06 and MNEQ09 that fell within one MNEQ unit were included in the analyses. We follow Eronen et al. (2009) in using genus-level data and including only mammal localities with seven or more genera. Due to the regional focus, we include three Damiao localities that have less than seven genera of large mammals. This is expected to make our similarity estimates less precise but in unlikely to bias them systematically.

Stable isotope analysis

Plants have distinct ratios of $^{13}C/^{12}C$ that are preserved in fossil tooth enamel allowing the study of their past distribution (Koch, 1998; Kohn and Cerling, 2002). Most trees, shrubs, and herbaceous dicots use the C3 photosynthetic pathway, giving forest ecosystems a C3 carbon isotope signature (Passey et al., 2009), while C4 plants are mainly warm season grasses with distributions related to the growing season (rainy season) temperature (Teeri and Stowe, 1976). The values of $\delta^{13}C$ of herbivorous mammal tooth enamel reveal the $\delta^{13}C$ value of diet, which in turn sheds light on the environment. For modern mammalian tooth enamel, $\delta^{13}C$ values of approximately -9 ‰ or lower are indicative of a C3-based diet, while $\delta^{13}C$ values of about -1 ‰ or higher indicate a C4-based diet. In water-stressed environments these cut-off values for pure C3 diets are higher, approximately -8 ‰ for modern, and -7 ‰ for Miocene fossil samples (the difference between modern and fossil being due to fluctuations in the $\delta^{13}C$ of atmospheric CO_2; e.g., Cerling et al., 1997; Passey et al., 2002, 2009), and higher values indicate drier conditions or a small fraction of C4 in the ecosystems. Fossil tooth enamel from Damiao localities was sampled by grinding the specimens with a

diamond-drill and collecting the resulting powder over weighing paper. Samples were pretreated with 3% H_2O_2 and 0.1M CH_3COOH buffer solution. Enamel samples were reacted at 90˚C in a common acid bath device (in 100% H_3PO_4) and the resulting CO_2 was analysed the samples on a Finnigan MAT 252 isotope ratio mass spectrometer at the University of Utah. Isotope values were normalized to NBS-19 carbonate reference material ($\delta^{13}C$ = 1.95 ‰ PDB) or to internal laboratory standards calibrated against NBS-19. The results are shown in Figure 4 and tested using a pair-wise Mann-Whitney test to detect possible differences between groups of mammals and different localities. Tooth enamel $\delta^{18}O$ values are reported as mineral-equivalent values using enamel-specific CO_2-mineral fractionation factors (sometimes called phosphoric acid fractionation factors) reported in Passey et al., 2007.

Results

Mean hypsodonty and mean annual precipitation

A total of 839 fossil localities were used for the hypsodonty and MAP analysis (SOM). Pliopithecoid localities show lower and more constant mean hypsodonty values compared to other locality types throughout the studied time interval (Figure 2). Pairwise Mann-Whitney tests show that the detected differences in hypsodonty values are significant for all other pairs of locality types except hominoid and non-primate localities (Table 2). Damiao has markedly lower mean hypsodonty values than most Tunggurian localities, with the exception of Tunggur-TMS and Tunggur-HU, which each have a mean hypsodonty of 1 (Table 1).

FIGURE 2

TABLE 1

TABLE 2

Hominoid and pliopithecoid localities both have high predicted mean annual precipitation, consistently higher than any other locality type (Figure 3). A Pairwise Mann-Whitney test shows that pliopithecoid and hominoid localities cannot be significantly distinguished from each other. However, all other pairs of localities are significantly different from each other (Table 2). For pliopithecoid localities the estimated precipitation level varies the least being consistently high throughout their time range, not decreasing when all other locality types show declines in their humidity (Figure 3).

FIGURE 3

Closer inspection of the MAP results for Chinese MNEQ06-09 localities reveals that non-primate localities have the widest range in mean annual precipitation ranging from 200 to 2300 mm. Pliopithecoid localities have the second widest range between 1300 and 2300 mm. However, only one hominoid locality qualified for the analysis and it has a MAP of about 2000 mm. No cercopithecoid localities were qualified for the analyses. The MAP for DM01 is about 1300 mm, which is the lowest of all pliopithecid localities in Asia but higher than most Tunggur localities and the other two Damiao localities (Table 1).

Faunal similarity

Thirteen small mammal and 16 large mammal localities from the middle Miocene and early late Miocene (MNEQ06-09) were analysed (Tables 3 to 6). DM01 is most similar to Tunggur localities, especially Tunggur-Moergen. Of primate localities, DM01 is most similar to the Junggar-Tieersihabahe pliopithecid locality from northwestern China, when the large mammal fauna is studied. Small mammals from Junggar-Tieersihabahe were too scarce to allow the locality to be analysed.

TABLE 3

TABLE 4

TABLE 5

TABLE 6

Tunggurian localities are dominated by grassland adapted small mammals such as Erinaceidae (*Mioechinus*), Dipodidae (*Heterosminthus* and *Protalactaga*), Ochotonidae (*Alloptox*, *Bellatona*, and *Desmatolagus*), and Cricetidae with high crowned teeth (*Gobicrictedon*, and *Plesiodipus*). Small mammals in DM01 are similar to Tunggur. Aquatic species in both Tunggur and Damiao are represented by Castoridae.

Isotopes

Early Miocene fossils have $\delta^{13}C$ values ranging from -7.3 ‰ to -10.9‰ with an average of -8.5 ‰, and $\delta^{18}O$ values ranging between -1.9‰ and -11.1‰ (Figure 4, Table 7). Middle Miocene localities have lower averages than at early Miocene for carbon and oxygen, -10.0 ‰ and -7.9 ‰, respectively. Also the ranges are larger, $\delta^{13}C$ from -7.2 ‰ to -13.4 ‰ and $\delta^{18}O$ from -0.1 ‰ to -11.8 ‰. The average of $\delta^{13}C$ for late Miocene localities is -8.7 ‰ with a range from -4.46 ‰ to -11.9 ‰. However, the range for late Miocene localities is from -7.3 ‰ to -11.9 ‰ with an average of -9.6‰ when the late late Miocene locality of UH Museum is excluded. $\delta^{18}O$ values range between -0.0 ‰ and -13.1 ‰ both with and without the late late Miocene locality, however the average is -7.8 ‰ with UH Museum and -8.4 ‰ without it. The modern sample has a range of $\delta^{13}C$ between -5.7 ‰ and -8.9 ‰, averaging -7.2 ‰ and $\delta^{18}O$ values between -0.4 ‰ and -7.1 ‰, with an average of -3.0 ‰. The mean $\delta^{13}C$ value for modern mammals is higher than at any Miocene localities, although artiodactyls from the late late Miocene UH Museum locality have higher average $\delta^{13}C$ than the modern artiodactyl samples. The mean $\delta^{18}O$ value for the modern sample is high, but not the highest. The isotope results (Figure 4) are shown separately for Artiodactyla and Proboscidea, and two families of Perissodactyla (i.e., Equidae and Rhinocerotidae). Pair-wise Mann-Whitney test show that there is little difference in $\delta^{13}C$ values between the groups, only Artiodactyla and Rhinocerotidae are significantly different from each other. $\delta^{18}O$ separates Artiodactyla from both Rhinocerotidae and Equidae with statistical significance (Table 8).

FIGURE 4

TABLE 7

TABLE 8

Discussion

Situated ca. 200 kilometres northeast of Damiao, the Tunggur area has several localities that seem to have had ideal environmental conditions for pliopithecids, but no primate fossils have been found. Undersampling is a possible, though unlikely explanation for the absence of primate fossils at Tunggur, given the large collection of fossils from this site. The Tunggur-Moergen locality in particular seems to have had favourable conditions for pliopithecoids, with the highest combined faunal similarity to Damiao (Tables 3 and 4), similar predicted MAP, and comparable $\delta^{13}C$ values (Zhang et al., 2009). However, on average MAP in Tunggur is lower than in DM01.

During the Miocene, the estimated MAP for different types of localities show high and stable pattern for pliopithecoid localities with only minor fluctuation through time. Similarly high MAP values for hominoid localities are observed, although towards the end of the Miocene there is clear distinction from the pliopithecoid localities (Figure 3). Even if pliopithecoid localities cannot be distinguished from hominoid localities with standard statistical significance, it is evident from the contrasting fates of the two clades that hominoid species were more adaptable to the progressively drying Miocene environment. When only Chinese MNEQ06-09 localities are examined, most primate localities are missing from the analysis and meaningful comparisons are not possible. However, several pliopithecoid localities are present and it can be seen that DM01 is the driest of them, but still more humid than most Tunggur localities regardless of the method used (Table 1). Nonetheless, both Tunggur-HU and Tunggur-TMS have a similar or higher predicted MAP than DM01, similar to other Chinese pliopithecoid localities. The faunal similarity between DM01 and Tunggur-HU is also high when large mammals are studied, although not as high as between DM01 and Tunggur-Moergen. Tunggur-TMS on the other hand shares no large mammals with DM01. Small mammals

from Tunggur-TMS and Tunggur-HU localities are too scarce to be included in the analyses. Interestingly, comparing MAP estimates of DM01 with the older DM16, and younger DM02 suggests that the area was more humid during the pliopitheocid occupancy than before or after.

Large mammals in Damiao show a relatively stable pattern of environmental conditions through the Miocene with cervoids as the dominant group. This precludes the inference of widespread grassland or desert environments for Damiao localities (Kaakinen et al., 2015). DM01 is dominated by forest and woodland adapted large mammals, like Cervidae (*Stephanocemas* and *Euprox*), Moschidae (*Micromeryx*), Proboscidea (gen. et. sp. indet.), and Pliopithecidae (gen. et. sp. indet.) indicating a warm and humid environment (Zhang and Harrison, 2008; Wang and Zhang, 2011; Kaakinen et al. 2015). Also the sedimentology of DM01, with abundant goethite and manganese occurrences, implies a more humid climate for the middle Miocene (Kaakinen et al., 2015).

The small mammals at both Damiao and Tunggur, on the other hand, are dominated by grassland-adapted taxa with some castorids indicating the presence of water (Table 6). The occurrence of dipodids and ochotonids together with Sciuridae (*Atlantoxerus*) may indicate a semidesert environment, as suggested for Tunggur (Qiu, 1996).

The isotope data from 12 Damiao localities show variation in $\delta^{13}C$ values between -4.5 ‰ and -13.4 ‰ indicating that large herbivorous mammals in Damiao were predominantly feeding on C3 plants or water-stressed C3 plants, while no pure C4 diets were consumed, similar to Tunggur (see Zhang et al., 2009). All of the $\delta^{13}C$ values higher than -7 ‰ are from the late late Miocene locality of UH Museum, suggesting that C4 vegetation was not a significant part of the diet of herbivores at Damiao until the latest Miocene. The presence of C4 vegetation at late late Miocene UH Museum site also fits the latitudinal profile of northward increasing $\delta^{13}C$ values during the late Miocene (Passey et al. 2009) showing that environments were more open to the north. This is consistent with other studies from central Inner Mongolia (Zhang et al., 2009), where the onset of C4 expansion has been dated to the late Miocene. However, in some cases the samples reach the higher limits of a pure C3 diet indicating either the presence of a small fraction of C4 vegetation

or water-stressed conditions with C3 plants displaying more enriched $\delta^{13}C$ values (Farquhar et al., 1989; Cerling et al., 1997; Wang et al., 2008). Variation between species (orders/families) in their $\delta^{13}C$ composition might imply mixed habitats, lower $\delta^{13}C$ values suggesting forests, while higher values suggest grasslands. However, the differences between herbivore groups were not statistically significant, except for Artiodactyla and Rhinocerotidae, suggesting similar conditions and habitat preferences for most species. Out of all the Damiao localities, the primate-bearing DM01 has the lowest $\delta^{13}C$ values, indicating the most humid relative conditions, but likely with locally a mixed habitat indicated by the wide range of $\delta^{13}C$ values. However, DM01 is statistically significantly different only from early Miocene DM16, late Miocene UH Museum, and the modern sample (Table 9).

TABLE 9

The wide range of $\delta^{18}O$ values for DM01 and other middle Miocene localities at Damiao may indicate seasonal aridity, with high values of $\delta^{18}O$ indicating more arid conditions, and low values suggesting more humid conditions (Sternberg et al., 1989; Quade et al., 1995; Cerling et al., 2004; Feranec and MacFadden, 2006). The highest values of $\delta^{18}O$ are seen in Artiodactyla, possibly because they were the most water-independent, able to subsist on water in plants in times of seasonal aridity, as are several species today (e.g. Western, 1975; Braun, 1999a, b, c). In oxygen isotopic composition Artiodactyla are significantly different from both Equidae and Rhinocerotidae, but not Proboscidea, which consists of only two samples (Table 8). Indeed, oxygen isotope data are most meaningful when normalized to contemporaneous meteoric water isotopic compositions, with greater deviations of enamel $\delta^{18}O$ relative to meteoric water (= higher absolute values of $\delta^{18}O$) being closely correlated with measures of environmental aridity such as PET – MAP (potential evapotranspiration minus mean annual precipitation; Levin et al., 2006). We do not have estimates of $\delta^{18}O$ contemporaneous meteoric water for the different time horizons represented at Damiao, but if we assume that $\delta^{18}O$ was constant through time, we can interpret $\delta^{18}O$ values directly as measures of aridity, with higher values indicating more arid conditions. Under this rubric, and restricting the analysis to Artiodactyls with $N \geq 2$ (as there is significant taxon-specific patterning in $\delta^{18}O$ data), the more arid intervals

are modern, UH Museum (late late Miocene), and DM02 (early late Miocene), whereas the more humid intervals are DM01 and DM03 (middle Miocene) as well as DM26 (late Miocene). These interpretations are preliminary only, and larger and more uniform sample sizes across different taxa at each locality will be necessary for more conclusive estimates of past aridity based on $\delta^{18}O$, as well as independent estimates of $\delta^{18}O$ of meteoric water for each locality.

The sedimentological data from the Damiao sequence suggest well-drained floodplains and groundwater evaporation, as evidenced by abundant red-brown fine-grained deposits with concentrations of nodular carbonates. Abundant goethite and manganese staining in the stacked carbonate nodule conglomerate at DM01 point to periodic wetting and drying of sediments (cf. Kraus and Hasiotis, 2006) suggesting relatively humid conditions locally. The abraded soil nodule clasts, however, arise from the reworking of underlying overbank deposits, indicating that climate was seasonally dry (cf. Van Itterbeeck et al., 2007; Kaakinen et al., 2015).

The presence of pliopithecoids, a clade that favours humid environments, in Central Asia after the middle Miocene climatic optimum seems incompatible with a trend of strengthening of climatic zones and increased aridification at mid latitudes in wide areas since the early Miocene (Kaakinen et al., 2015). It is, however, consistent with the hypsodonty and estimated MAP values suggesting more humid and possibly more wooded environments for the DM01 pliopithecoid locality. Evidence for warm and humid environments for DM01 also includes the presence of an anchitheriine horse and the cervid *Euprox altus*, as well as the occurrence of abundant goethite and manganese staining commonly attributed to impeded drainage (Kaakinen et al., 2015). Regional interpretation of large mammal proxy data by Liu et al. (2009) supports this scenario by providing evidence of humid areas in the northern parts of China, while a distinctive dry belt developed in the mid latitudes. The isotopic evidence does not support constantly humid environments, but is compatible with a scenario of a more humid climate with pronounced dry season, or a generally semi-arid habitat with heavily vegetated belts around permanent waterways.

Seasonally dry climate may also be inferred from the reworked pedogenic nodules in the DM01 conglomerates (Kaakinen et al., 2015, Van Itterbeeck et al., 2007).

Conclusions

Our analyses of the palaeoecology of the late middle Miocene pliopithecoid locality DM01 support previous inferences concerning the presence of locally humid environments within the increasingly arid surroundings that characterized Central Asia. Hypsodonty, and estimated MAP, combined with local sedimentology and the community structure of large mammals suggest more humid and possibly more forested and wooded environments for DM01. However, the small mammal fauna and isotope data are consistent with a mosaic of forest and grassland environment for all Damiao localities.

Based on the results presented here, Tunggur may have been too seasonal or not sufficiently humid for pliopithecoids. This inference is supported by the higher mean hypsodonty and lower predicted MAP estimates, as well as the slightly higher $\delta^{13}C$ values. We conclude that DM01, the driest known Asian pliopithecoid locality, may have been a more humid refugium within a generally drier regional setting, similar to some of the late late Miocene hominoid localities of western Asia (Kaya et al., 2016, Mirzaie Ataabadi et al., 2016). Although humid favouring as a clade, there were pliopithecoids that were able tolerate some level of seasonal dryness as evidenced in Damiao.

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FIGURE 1. A. Damiao and Tunggur localities. b. Damiao localities

FIGURE 2. Mean hypsodonty curves from different types of fossil localities at different MNEQ intervals (smoothing spline fit with λ=10). DM01 and Tunggur localities plotted individually.

FIGURE 3. Mean annual precipitation curves from different types of fossil localities at different MNEQ intervals (smoothing spline fit with λ=10). DM01 and Tunggur localities plotted individually (smoothing spline fit with λ=10).

FIGURE 4. Carbon and oxygen isotope values for Damiao fossil localities and a modern sample. All known palaeomagnetic ages for the individual localities are shown on the right column. (?=eocene locality). The predicted $\delta^{13}C$ values for pure C_3 diets (vertical dashed lines in the $\delta^{13}C$ plot) are based on passey et al. (2002, 2009). the vertical dashed line in the $\delta^{18}O$ plot shows the highest $\delta^{18}O$ value observed for a non-artiodactyl, highlighting the high $\delta^{18}O$ space (right of the dashed line) which is the exclusive domain of artiodactyls.

TABLE 1.

NAME	LocTYPE	MNEQ	MeanHYP	MAP (Liu et al., 2012)	MAP (Eronen et al., 2010)
Jiulongkou	NONPRIM	MNEQ06	1.22	886.96	1939.00
Junggar-Botamoyin	NONPRIM	MNEQ06	1.00	1241.18	1939.00
Junggar-botamoyindong	NONPRIM	MNEQ06	1.00	596.40	733.10
Junggar-chibaerwoyi	NONPRIM	MNEQ06	1.00	1284.16	733.10
Junggar-Ganqikairixi	NONPRIM	MNEQ06	1.00	882.97	733.10
Lantian-koujiacun	NONPRIM	MNEQ06	1.00	2315.80	733.10
Liuhe-lingyanshan	NONPRIM	MNEQ06	1.00	2029.23	733.10
Qaidam-Olongbuluk	NONPRIM	MNEQ06	1.40	603.58	399.70
Tairum Nor	NONPRIM	MNEQ06	1.40	947.46	399.70
Tongxin-dingjiaergou	NONPRIM	MNEQ06	1.29	1230.95	1405.00
Tongxin-gujiazhuang	NONPRIM	MNEQ06	1.00	2315.80	733.10
Tongxin-jinzuizigou	NONPRIM	MNEQ06	1.00	2315.80	733.10
Tongxin-shataigou	NONPRIM	MNEQ06	1.00	2315.80	733.10
Tongxin-Yehuliquezi	NONPRIM	MNEQ06	1.00	2315.80	733.10
Hezheng-laogou	PLIO	MNEQ06	1.36	1540.78	1939.00
Junggar-Tieersihababahe	PLIO	MNEQ06	1.00	1599.38	1405.00
Tongxin	PLIO	MNEQ06	1.67	1468.07	399.70
Tongxin-maerzuizigou	PLIO	MNEQ06	1.00	2315.80	733.10
Kaiyuan-Xiaolongtan	HOMIN	MNEQ07/8	1.00	1947.36	1405.00
Fangxian	NONPRIM	MNEQ07/8	1.80	1126.58	399.70
Junggar-duolebulejin	NONPRIM	MNEQ07/8	1.75	1147.18	681.60
Junggur_dingshanyanchi	NONPRIM	MNEQ07/8	1.00	882.97	733.10
Lantian-gaopo-64004	NONPRIM	MNEQ07/8	1.67	894.93	399.70
Lantian-gaopo-64008	NONPRIM	MNEQ07/8	1.50	1250.15	399.70
Lanzhou-Quantougou	NONPRIM	MNEQ07/8	1.00	2029.23	733.10
Lintong-lengshuigou	NONPRIM	MNEQ07/8	1.73	869.97	399.70
Minhe-lierbao	NONPRIM	MNEQ07/8	1.50	1250.15	399.70
Minhe-nanhawangou	NONPRIM	MNEQ07/8	1.50	1250.15	399.70
Tunggur- ALU	NONPRIM	MNEQ07/8	1.57	483.84	399.70
Tunggur- DA	NONPRIM	MNEQ07/8	1.40	775.52	399.70
Tunggur- HU	NONPRIM	MNEQ07/8	1.00	1360.58	1939.00
Tunggur- MC	NONPRIM	MNEQ07/8	1.80	840.01	399.70
Tunggur- MOII	NONPRIM	MNEQ07/8	1.67	894.93	399.70
Tunggur- PQ	NONPRIM	MNEQ07/8	2.00	1044.20	200.90
Tunggur- TMS	NONPRIM	MNEQ07/8	1.00	1885.95	733.10
Tunggur- ZH	NONPRIM	MNEQ07/8	1.50	820.30	399.70
Tunggur-AC	NONPRIM	MNEQ07/8	1.67	1181.50	399.70
Tunggur-Moergen	NONPRIM	MNEQ07/8	1.33	1092.56	1426.00
Tunggur-WC	NONPRIM	MNEQ07/8	1.67	1009.56	399.70
Xinan	NONPRIM	MNEQ07/8	1.50	1078.21	399.70
DM01	PLIO	MNEQ07/8	1.00	1284.16	1405.00
DM02	NONPRIM	MNEQ07/8	1.00	596.40	733.1
Amuwusu	NONPRIM	MNEQ09	1.00	1026.25	733.10
Dongxiang-wangji	NONPRIM	MNEQ09	3.00	202.45	200.90
Guonigou	NONPRIM	MNEQ09	2.57	593.90	200.90
Lantian-12	NONPRIM	MNEQ09	2.00	471.07	200.90
Qaidam-Tuosu	NONPRIM	MNEQ09	2.00	399.43	399.70
Wuzhong-ganhegou	NONPRIM	MNEQ09	1.75	932.25	681.60
Zhongning-ganhegou	NONPRIM	MNEQ09	2.33	906.90	200.90

TABLE 1. Mean hypsodonty and mean annual precipitations for Chinese MNEQ06-09 localities.

TABLE 2

MAP \ HYP	CERCO	HOMIN	NON-PRIM	PLIO
CERCO		**0.00**	**0.00**	**0.00**
HOMIN	**0.00**		0.11	**0.00**
NON-PRIM	**0.00**	**0.00**		**0.00**
PLIO	**0.00**	0.23	**0.00**	

Significant values in bold.

TABLE 2. P-values for Mann-Whitney pair-wise test of mean hypsodonty and mean annual precipitation of different types of localities (MAP at lower left, HYP at upper right).

1 TABLE 3

	DM01
DM01	-
DM02	1.00
Hezheng-laogou	0.25
Jiulongkou	0.25
Junggar-Botamoyin	0.25
Junggar-Tieersihabahe	0.50
Tairum Nor	0.25
Tongxin	0.25
Tongxin-dingjiaergou	0.25
Junggar-duolebulejin	0.25
Lintong-lengshuigou	0.25
Tunggur- ALU	0.50
Tunggur- HU	0.50
Tunggur- ZH	0.25
Tunggur-Moergen	0.75
Tunggur-WC	0.00

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3

4 TABLE 3. Simpson similarity indices for large mammal faunas from Chinese localities within MNEQ06-09.

5

1

2 TABLE 4

	DM01
DM01	-
DM02	0.55
Sunite-Chagannuoer	0.67
Tairum Nor	0.44
Junggar_dingshanyanchi_XJ20061	0.46
Junggur_dingshanyanchi	0.43
Lanzhou-Quantougou	0.43
Tunggur- 482	0.63
Tunggur- MOII	0.76
Tunggur- MOV	0.73
Tunggur- TLR	0.55
Tunggur- TUR	0.65
Tunggur-Moergen	0.82

3

4

5 TABLE 4. Simpson similarity indices for small mammal faunas from Chinese localities within MNEQ06-09.

6

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TABLE 5

	DM 01	DM16	DM02	Tunggur- ALU	Tunggur- DA	Tunggur- HU	Tunggur- MC	Tunggur- MOII	Tunggur- PQ	Tunggur- TMS	Tunggur- ZH	Tunggur-AC	Tunggur-Moergen	Tunggur-WC
Acerorhinus	0	0	0	1	0	0	1	0	0	1	0	0	1	1
Aelurocyon	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Amphicyon	0	0	0	1	0	0	0	0	0	0	0	0	1	0
Anchitherium	0	0	0	0	0	1	0	0	0	0	0	1	1	1
Chalicotherium	0	0	0	0	0	1	0	0	0	0	0	0	1	1
Dicrocerus	0	0	0	1	1	1	1	1	0	0	0	0	1	0
Euprox	1	0	1	1	0	1	0	0	0	0	0	0	1	0
Gobicyon	0	0	0	0	0	0	0	0	0	0	1	0	1	1
Hispanotherium	0	0	0	0	0	0	1	0	1	0	0	0	1	1
Kubanochoerus	0	0	0	0	0	1	0	0	0	0	0	0	1	0
Lagomeryx	0	1	0	0	0	1	0	0	0	0	1	0	1	0
Leptarctus	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Listriodon	0	0	0	0	0	0	0	0	0	0	0	0	1	1
Martes	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Melodon	0	0	0	0	0	1	1	0	0	0	1	0	1	0
Metacervulus	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Metailurus	0	0	0	0	0	1	0	0	0	0	0	0	1	1
Micromeryx	1	1	1	0	1	0	0	0	0	0	0	0	1	0
Mionictis	0	0	0	0	0	0	0	0	0	0	1	0	1	0
Palaeotragus	0	0	0	0	0	0	0	0	0	0	0	0	1	1
Percrocuta	0	0	0	1	0	0	0	0	0	0	0	1	1	1
Platybelodon	0	0	0	0	1	1	1	1	1	1	0	1	1	1
Pliopithecus	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Plithocyon	0	0	0	0	0	0	0	0	0	0	0	1	1	1
Pseudarctos	0	0	0	1	0	0	0	0	0	0	0	0	1	0
Sansanosmilus	0	0	0	1	0	0	0	0	1	0	0	0	1	0
Serridentinus	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Stephanocemas	1	1	1	1	1	1	0	0	0	0	1	0	1	0
Sthenictis	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Tungurictis	0	0	0	1	0	1	0	0	0	1	0	0	1	1
Turcocerus	0	0	0	1	1	0	1	1	0	0	1	1	1	1
Zygolophodon	0	0	0	0	0	1	0	0	0	0	0	0	1	0

TABLE 5. Large mammal fauna at Damiao and Tunggur.

1 TABLE 6

	DM01	DM16	DM02	Tunggur- 482	Tunggur- HU	Tunggur- MOII	Tunggur- MOV	Tunggur- TLR	Tunggur- TUR	Tunggur-AC	Tunggur-Moergen	Tunggur-Tamuqin	Tunggur-WC
Alloptox	0	0	1	1	0	1	1	1	1	0	1	0	0
Anchitheriomys	0	0	0	0	1	0	0	0	0	0	1	0	0
Ansomys	1	0	0	0	0	0	1	0	1	0	1	0	0
Atelerix	0	0	0	0	0	0	0	0	0	0	1	0	0
Atlantoxerus	1	0	0	1	0	1	0	1	1	0	1	0	0
Bellatona	1	0	1	1	0	1	1	1	1	1	1	1	0
Democricetodon	1	0	0	0	0	1	1	0	0	0	1	0	0
Desmanella	1	0	0	0	0	1	0	0	0	0	1	0	0
Desmatolagus	1	0	1	1	0	1	0	1	0	0	1	0	0
Distylomys	0	1	0	0	0	0	0	1	0	0	0	0	0
Eozapus	0	0	1	0	0	0	0	0	0	0	0	0	0
Eucastor	1	0	0	0	0	0	0	0	0	0	0	0	0
Eutamias	1	0	0	0	0	1	1	0	1	0	1	0	0
Gobicricetodon	1	0	1	0	1	1	1	1	1	0	1	1	0
Heterosminthus	1	1	0	1	1	1	1	1	1	0	1	0	1
Hystricops	0	0	0	0	0	0	0	0	0	1	0	0	0
Keramidomys	1	0	0	0	0	1	0	0	1	0	1	0	0
Kherem	0	1	0	0	0	0	0	0	0	0	0	0	0
Leptodontomys	1	0	0	0	0	1	0	0	1	0	1	0	0
Lophocricetus	0	0	1	0	0	0	0	0	0	0	0	0	0
Megacricetodon	0	0	0	1	0	1	1	1	1	0	1	0	0
Metexallerix	0	1	0	0	0	0	0	0	0	0	0	0	0
Microdyromys	1	0	0	0	0	1	0	0	1	0	1	0	0
Mioechinus	1	0	1	1	0	1	1	1	1	0	1	0	0
Mongolosorex	0	0	0	0	0	1	0	0	1	0	1	0	0
Monosaulax	0	0	0	0	1	1	0	0	0	1	0	0	0
Nannocricetus	0	0	1	0	0	0	0	0	0	0	0	0	0
Ochotona	1	0	1	0	0	0	0	0	0	0	0	0	0
Plesiodipus	1	0	0	0	0	1	1	1	1	0	1	1	1
Plesiosminthus	0	1	0	0	0	0	0	0	0	0	0	0	0
Prodistylomys	0	1	0	0	0	0	0	0	0	0	0	0	0
Proscapanus	0	0	0	0	0	1	0	0	1	0	1	0	0
Prosiphneus	1	0	0	0	0	0	0	0	0	0	0	0	0
Prosphneus	0	0	1	0	0	0	0	0	0	0	0	0	0
Protalactaga	1	0	1	1	0	1	1	0	1	0	1	0	0
Pseudotheridomys	0	1	0	0	0	0	0	0	0	0	0	0	0
Quyania	0	0	0	0	0	1	0	0	0	0	1	0	0
Sinodonomys	0	1	0	0	0	0	0	0	0	0	0	0	0
Sinolagomys	0	1	0	0	0	0	0	0	0	0	0	0	0
Sinotamias	0	0	0	0	0	1	0	0	1	0	1	0	0
Steneofiber	1	0	0	0	0	0	0	0	0	0	0	1	0

Tachyoryctoides	0	1	0	0	0	0	0	1	0	0	0	0	0
Trogontherium	0	0	0	0	0	0	0	0	0	0	1	0	0
Yanshuella	0	0	0	0	0	1	0	0	1	0	1	0	0

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3 TABLE 6. Small mammal fauna at Damiao and Tunggur.

4

Table

1 TABLE 7

SAMPLE ID	FAMILY	ORDER	LOCALITY	AGE	δ^{13}C PDB	δ^{18}O PDB
DM.15.113	Artiodactyla	Cervidae	15	early Miocene	-8.8	-1.9
DM.16.254 rhino	Perissodactyla	Rhinocerotidae	16	early Miocene	-7.3	-10.4
DM.16.115	Perissodactyla	Rhinocerotidae	16	early Miocene	-7.4	-9.2
DM.16.291 rhino	Perissodactyla	Rhinocerotidae	16	early Miocene	-8.1	-9.9
DM.16.294 rhino	Perissodactyla	Rhinocerotidae	16	early Miocene	-8.1	-11.1
DM.16.255 rhino	Perissodactyla	Rhinocerotidae	16	early Miocene	-9.1	-9.2
DM.17.186.2	Perissodactyla	Rhinocerotidae	17	early Miocene	-7.8	-8.6
DM.17.175	Perissodactyla	Rhinocerotidae	17	early Miocene	-8.4	-7.3
DM.17.174	Perissodactyla	Rhinocerotidae	17	early Miocene	-8.9	-6.2
DM.17.186.1	Perissodactyla	Rhinocerotidae	17	early Miocene	-9.0	-8.3
DM.17.176.1	Perissodactyla	Rhinocerotidae	17	early Miocene	-11.0	-4.4
DM.01.199.1	Perissodactyla	Rhinocerotidae	1	middle Miocene	-7.2	-5.4
DM.01.196	Artiodactyla	Bovidae	1	middle Miocene	-8.2	-3.7
DM.01.206	Perissodactyla	Rhinocerotidae	1	middle Miocene	-8.2	-8.3
DM.01.70	Artiodactyla	Cervidae	1	middle Miocene	-8.6	-3.8
DM.01.137	Perissodactyla	Rhinocerotidae	1	middle Miocene	-9.7	-6.1
DM.01.77	Perissodactyla	Rhinocerotidae	1	middle Miocene	-10.3	-10.1
DM.01.135	Artiodactyla	Cervidae	1	middle Miocene	-10.7	-11.8
DM.01.198	Perissodactyla	Rhinocerotidae	1	middle Miocene	-11.0	-8.2
DM.01.91	Perissodactyla	Rhinocerotidae	1	middle Miocene	-11.1	-10.3
DM.01.99	Perissodactyla	Rhinocerotidae	1	middle Miocene	-11.3	-10.3
DM.01.197	Perissodactyla	Rhinocerotidae	1	middle Miocene	-11.3	-9.3
DM.01.207.1	Perissodactyla	Rhinocerotidae	1	middle Miocene	-11.8	-8.6
DM.01.123	Artiodactyla		1	middle Miocene	-13.4	-7.2
DM.03.132.2	Artiodactyla		3	middle Miocene	-7.4	-0.1
DM.03.132.1	Artiodactyla		3	middle Miocene	-7.9	-7.5
DM.03.128	Artiodactyla	Cervidae	3	middle Miocene	-10.0	-10.0
DM.03.127.2	Perissodactyla	Rhinocerotidae	3	middle Miocene	-10.8	-6.0
DM.03.127.1	Perissodactyla	Rhinocerotidae	3	middle Miocene	-10.9	-9.9
DM.03.130	Artiodactyla		3	middle Miocene	-11.0	-10.0
DM.03.131	Artiodactyla		3	middle Miocene	-11.2	-11.2
DM.09.25	Proboscidea	Gomphotheriidae	9	middle Miocene	-7.5	-5.3
DM.09.27	Proboscidea	Gomphotheriidae	9	middle Miocene	-9.6	-11.0
DM.02.61	Artiodactyla	Bovidae	2	late Miocene	-7.3	-2.3
DM.02.48	Artiodactyla	Bovidae	2	late Miocene	-7.7	-0.0
DM.06.155	Perissodactyla	Rhinocerotidae	6	late Miocene	-8.4	-8.2
DM.06.153	Perissodactyla	Equidae	6	late Miocene	-9.8	-8.2
DM.06.139.2	Perissodactyla	Rhinocerotidae	6	late Miocene	-9.9	-9.5
DM.06.157	Perissodactyla	Equidae	6	late Miocene	-10.7	-8.4
DM.06.156.1	Perissodactyla	Rhinocerotidae	6	late Miocene	-11.5	-10.5
DM.06.139.1	Perissodactyla	Rhinocerotidae	6	late Miocene	-11.6	-7.8
DM.06.156.2	Perissodactyla	Rhinocerotidae	6	late Miocene	-11.6	-10.9
DM.06.156.3	Perissodactyla	Rhinocerotidae	6	late Miocene	-11.7	-8.4
DM.06.138	Perissodactyla	Rhinocerotidae	6	late Miocene	-11.9	-9.7
DM.06.158.1	Perissodactyla	Rhinocerotidae	6	late Miocene	-12.0	-10.1
DM.12.104	Perissodactyla	Rhinocerotidae	12	late Miocene	-8.2	-10.6

DM.12.103	Perissodactyla	Rhinocerotidae	12	late Miocene	-8.4	-7.9
DM.12.100	Perissodactyla	Rhinocerotidae	12	late Miocene	-8.5	-11.7
DM.12.102	Perissodactyla	Rhinocerotidae	12	late Miocene	-8.5	-10.2
DM.12.101	Perissodactyla	Rhinocerotidae	12	late Miocene	-11.1	-5.9
DM.13.37	Perissodactyla	Rhinocerotidae	13	late Miocene	-8.1	-10.6
DM.13.34	Perissodactyla	Equidae	13	late Miocene	-8.7	-6.1
DM.13.30	Perissodactyla	Rhinocerotidae	13	late Miocene	-8.9	-9.6
DM.13.28	Perissodactyla	Equidae	13	late Miocene	-9.5	-10.6
DM.13.38	Perissodactyla	Rhinocerotidae	13	late Miocene	-10.7	-8.4
DM.26.BHP-3	Artiodactyla	Bovidae	26	late Miocene	-7.8	-13.1
DM.26.BHP-2	Perissodactyla	Rhinocerotidae	26	late Miocene	-8.1	-8.8
DM.26-BHP-6	Perissodactyla	Rhinocerotidae	26	late Miocene	-8.5	-11.2
DM.26-BHP-7	Artiodactyla	Bovidae	26	late Miocene	-8.6	-3.1
DM.26.BHP-4	Perissodactyla	Equidae	26	late Miocene	-9.6	-5.0
DM.26.BHP-1	Perissodactyla	Equidae	26	late Miocene	-9.9	-8.7
DM.26.BHP-5	Perissodactyla	Equidae	26	late Miocene	-10.1	-8.4
CN2008-UH-192	Artiodactyla	Bovidae	UH Museum	late late Miocene	-4.5	-2.4
CN2008-UH-201	Artiodactyla	Bovidae	UH Museum	late late Miocene	-4.9	-10.8
CN2008-UH-194	Artiodactyla	Giraffidae	UH Museum	late late Miocene	-6.3	-5.1
CN2008-UH-193	Artiodactyla	Bovidae	UH Museum	late late Miocene	-6.6	-1.1
CN2008-UH-200	Artiodactyla	Bovidae	UH Museum	late late Miocene	-6.7	-3.8
CN2008-UH-199	Artiodactyla	Bovidae	UH Museum	late late Miocene	-6.8	-1.1
CN2008-UH-198	Perissodactyla	Equidae	UH Museum	late late Miocene	-7.0	-8.4
CN2008-UH-196	Perissodactyla	Equidae	UH Museum	late late Miocene	-7.0	-9.1
CN2008-UH-197	Perissodactyla	Equidae	UH Museum	late late Miocene	-7.4	-8.7
CN2008-UH-190	Perissodactyla	Rhinocerotidae	UH Museum	late late Miocene	-7.6	-7.9
CN2008-UH-191	Perissodactyla	Rhinocerotidae	UH Museum	late late Miocene	-7.7	-8.2
CN2008-UH-195	Perissodactyla	Equidae	UH Museum	late late Miocene	-8.2	-8.7
CN2008-DM-188	Artiodactyla	Bovidae	modern	Modern	-5.7	-0.5
CN2008-DM-189	Artiodactyla	Bovidae	modern	Modern	-6.2	-3.9
CN2008-DM-187	Artiodactyla	Bovidae	modern	Modern	-6.8	-7.1
CN2008-DM-186	Artiodactyla	Bovidae	modern	Modern	-8.5	-0.4
CN2008-DM-109	Artiodactyla	Bovidae	modern	Modern	-8.9	-2.9

TABLE 7. Carbon and oxygen isotope values for Damiao fossil localities and modern samples.

TABLE 8

$\delta^{13}C$ \ $\delta^{18}O$	Artiodactyla	Proboscidea	Equidae	Rhinocerotidae
Artiodactyla		0.24	**0.02**	**0.00**
Proboscidae	0.61		0.92	0.93
Equidae	0.11	0.92		0.27
Rhinocerotidae	**0.00**	0.37	0.24	

Significant values in bold.

TABLE 8. P-values for Mann-Whitney pair-wise test of stable isotopes of different groups of large herbivorous mammals (δ^{13}c at lower left, and δ^{18}o at upper right).

Table

TABLE 9

$\delta^{13}C \setminus \delta^{18}O$	MODERN	LATE MIOCENE						MIDDLE MIOCENE			EARLY MIOCENE		EOCENE?
		DM02	DM06	DM12	DM13	DM26	UH	DM01	DM03	DM09	DM15	DM16	DM17
MODERN		0,33	**0**	**0,02**	**0,02**	**0,02**	0,07	**0,01**	0,07	0,18	1	**0,01**	**0,02**
DM02	0,85		**0,04**	0,08	0,08	0,06	0,08	**0,03**	0,11	0,25	0,54	0,08	0,07
DM06	**0,01**	**0,04**		0,76	0,71	0,92	0,08	0,34	0,73	0,91	0,15	0,24	0,12
DM12	0,3	0,08	**0,03**		1	0,75	0,13	0,38	0,42	0,85	0,24	1	0,24
DM13	0,09	0,08	**0,02**	0,53		0,75	0,13	0,3	0,75	0,85	0,24	0,68	0,24
DM26	0,07	0,06	**0,01**	0,81	0,75		0,22	0,75	1	0,88	0,19	0,26	0,43
UH	0,71	0,32	**0**	**0**	**0**	**0**		0,29	0,29	0,41	0,35	**0,01**	0,74
DM01	**0,01**	0,07	0,17	0,24	0,2	0,07	**0**		0,94	0,93	0,14	0,11	0,63
DM03	**0,03**	0,11	0,13	0,63	0,33	0,2	**0**	0,58		0,88	0,38	0,63	0,43
DM09	0,33	0,7	0,07	0,85	0,85	0,66	0,12	0,2	0,31		0,54	0,85	0,87
DM15	0,56	0,54	0,27	0,56	1	1	0,14	0,62	0,66	0,54		0,24	0,21
DM16	0,4	0,33	**0**	0,09	0,09	0,07	**0,03**	**0,02**	0,1	0,56	0,56		**0,04**
DM17	0,09	0,08	**0,03**	0,92	1	1	**0**	0,2	0,42	0,85	1	0,21	

Significant values in bold.

TABLE 9. P-values for Mann-Whitney pair-wise test of stable isotopes of different localities (δ^{13}c at lower left, and δ^{18}o at upper right).

Figure

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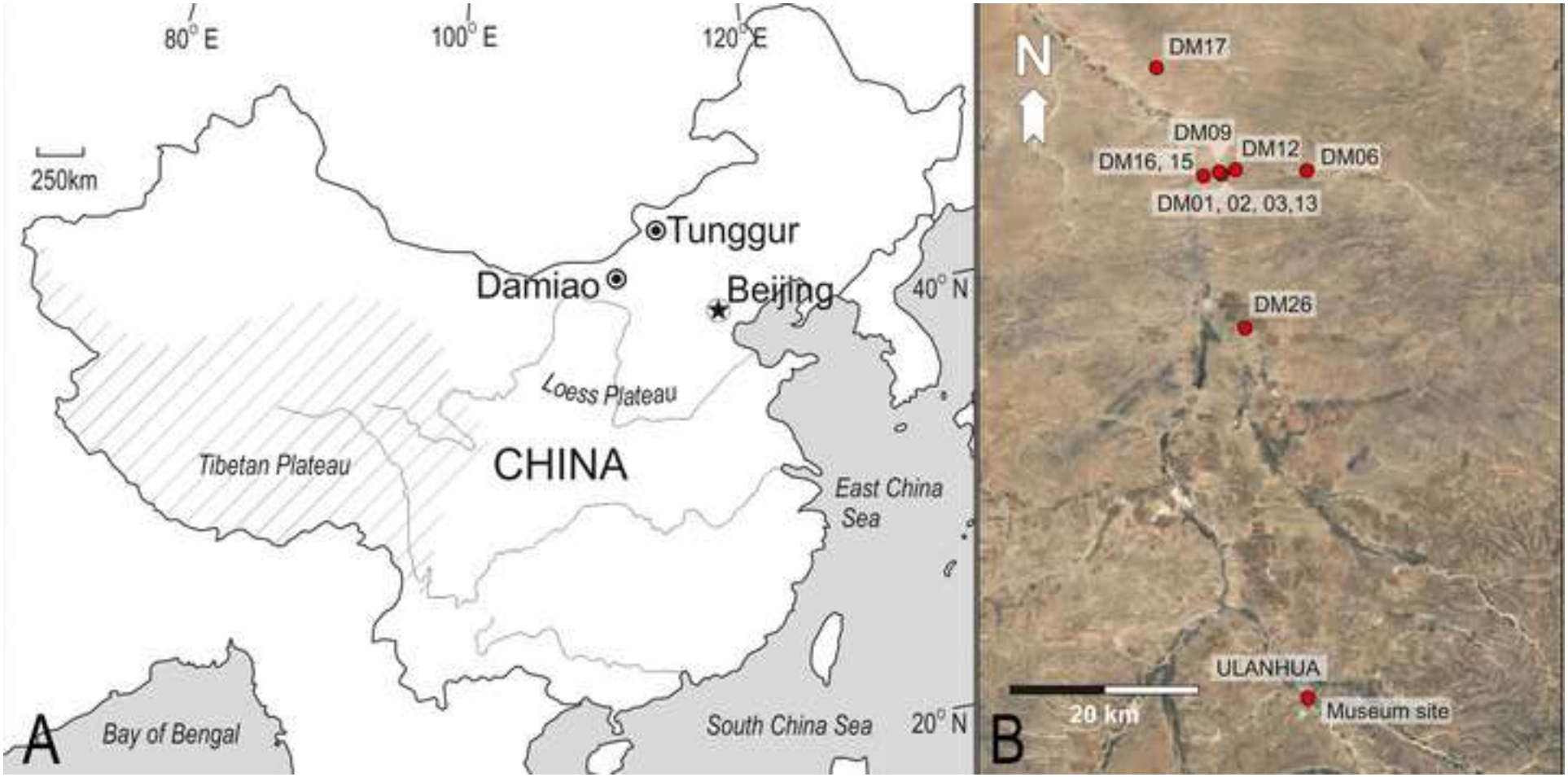

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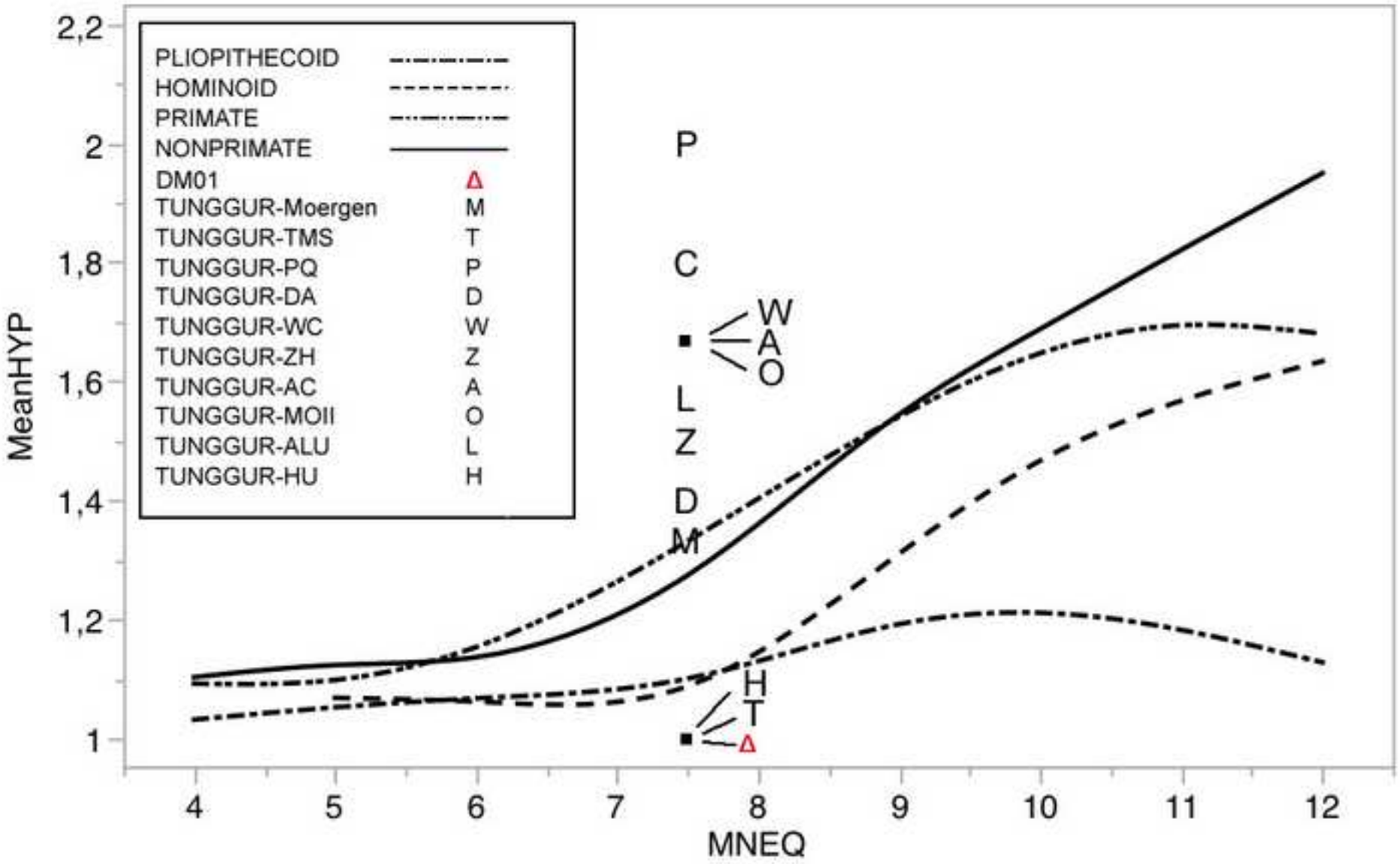

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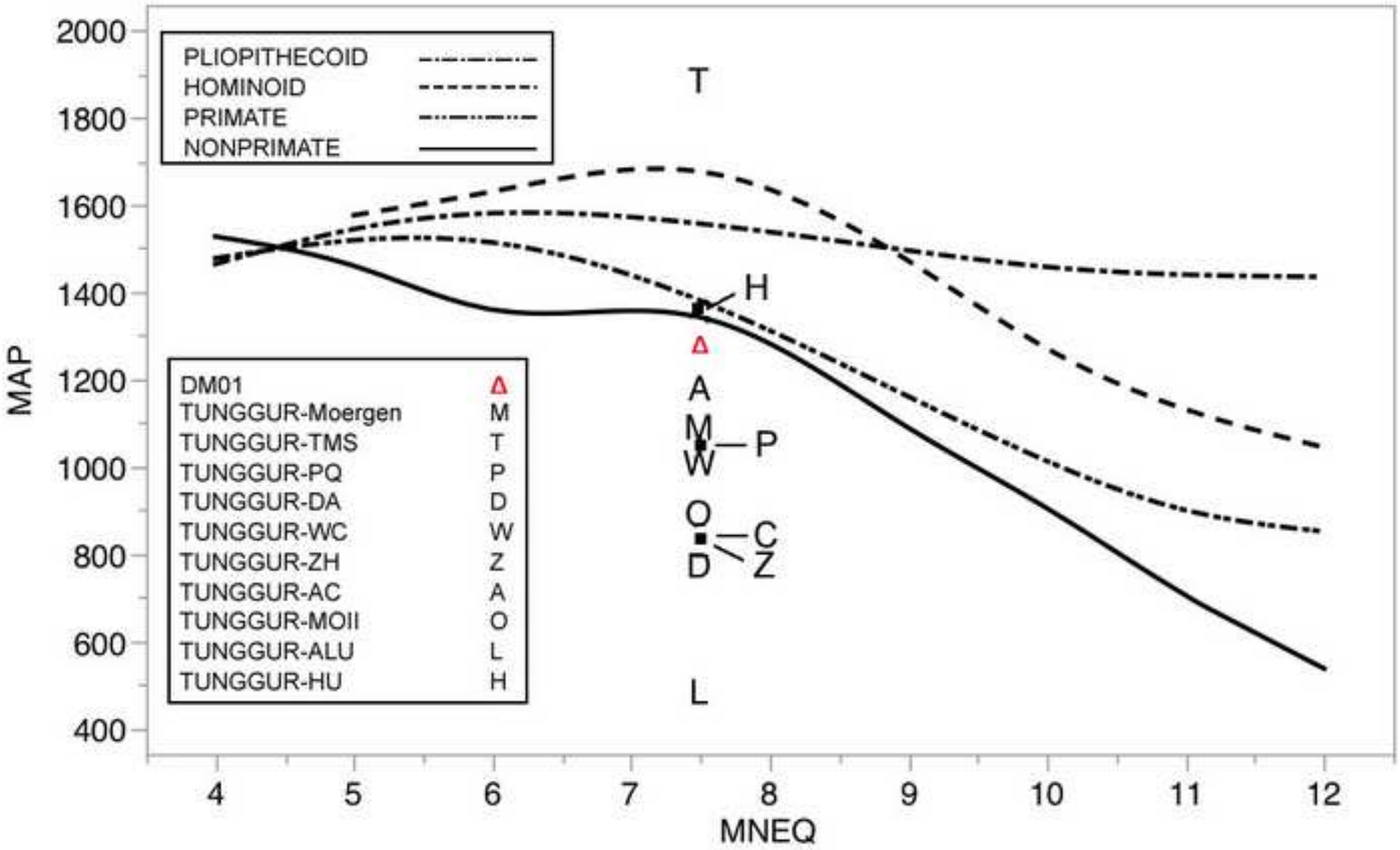

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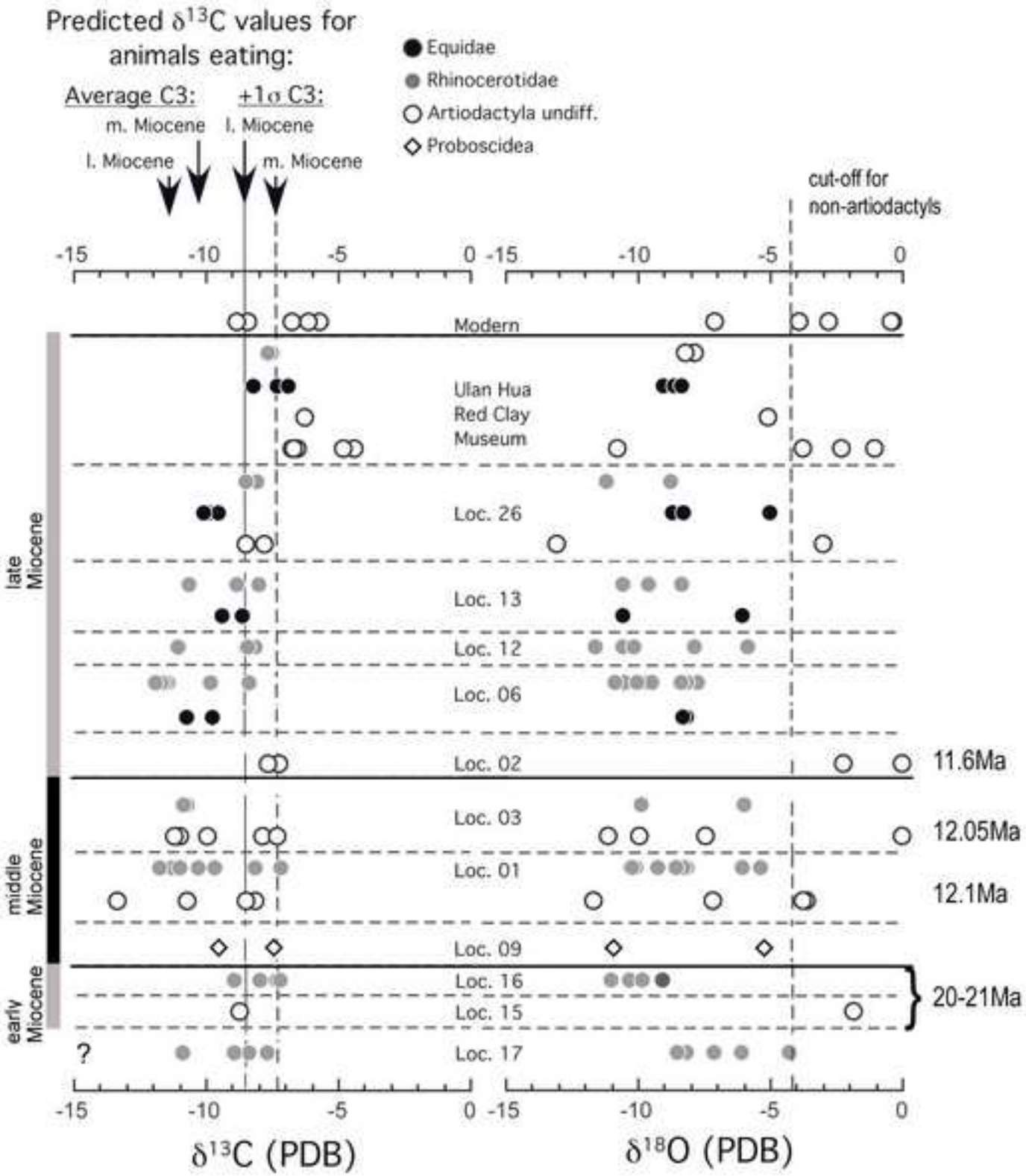

Supplementary Material

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